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Endolithic trace fossils in Ordovician-Silurian corals and stromatoporoids, Anticosti Island, eastern Canada

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ABSTRACT

Bioerosion was a significant process in the destruction of reef-building skeletons in early and mid-Paleozoic marine carbonate settings. Ordovician-Silurian corals and stromatoporoids from Anticosti Island show a limited diversity of macroborings, dominated by *Trypanites*, but also includes rare occurrences of an Ordovician bivalve boring (*Petroxestes pera*), described here for the first time in Early Silurian stromatoporoids. Two problematic embedment structures, one containing lingulid brachiopods, resemble borings but did not contribute to bioerosion. The distribution of the embedment structures and *Petroxestes pera* are restricted by facies and skeletal substrate. *Trypanites* is relatively nonspecific, occurring in reef and off-reef facies and in most skeletal substrates; it does not appear to have been affected by the Late Ordovician mass extinction.

Key words: Bioerosion. Boring. Paleozoic. Bivalve. *Trypanites*. *Petroxestes*.

RESUMEN

La bioerosión fue un proceso significativo en la destrucción de esqueletos de organismos constructores de arrecifes en medios carbonatados marinos en el Paleozoico inferior y medio. Los corales y estromatoporoideos del Ordovíco-Silúrico de Anticosti Island (Este del Canadá) muestran una limitada diversidad de macroperforaciones, dominadas por *Trypanites*, aunque también incluye algunos casos de perforaciones de bivalvos (*Petroxestes pera*), descritas aquí por primera vez en estromatoporoideos del Silúrico inferior. Dos estructuras de incrustación problemáticas, de las cuales una contiene braquiópodos lingúlidos, parecen perforaciones pero no contribuyeron a la bioerosión. La distribución de las estructuras de incrustación y de *Petroxestes pera* están restringidas a determinadas facies y substratos esqueléticos. *Trypanites* no muestra esa restricción, y aparece tanto en facies de arrecife como de *off-reef* y en la mayoría de los substratos esqueléticos; además, no parece haber sido afectado por la extinción masiva del Ordovícico superior.

Palabras clave: Bioerosión. Perforación. Paleozoico. Bivalvo. *Trypanites. Petroxestes*.

INTRODUCTION

Macroborings have a long geological record. The earliest were recognized in Early Cambrian rocks as simple *Trypanites* borings, which may have been made by sipunculid or polychaete worms at the tops of archaeocyathid reefs (James et al., 1977). Following this beginning, various organisms became capable of boring, leaving a legacy of diverse traces through the Early Paleozoic (for summaries see Kobluk et al., 1978; Palmer, 1982; Vogel, 1993). Cavities produced in a hard substrate by the deflection of the host substrate rather than by excavation (i.e. borings) are classified as embedment structures (Bromley, 1970; Ekdale et al., 1984). Since substrate material is not removed by embedment structures, they do not contribute to bioerosion.

Despite its long geologic history, much of bioerosion research has focused on modern carbonates, which are dominated by the bioeroding activity of infaunal sponges, bivalves, and gastropods, as well as the epifaunal grazing activity of fish and echinoderms. In order to characterize and quantify bioerosion in the fossil record, the Ordovician-Silurian of Anticosti Island was chosen for an extensive study of early borers. This paper describes the macroborings and embedment structures found in that study.

GEOLOGICAL SETTING

Anticosti Island (49°30'N, 63°00'W) displays a nearly continuous Late Ordovician-Early Silurian sequence of limestones and minor calcareous shales deposited in a subtropical to tropical carbonate ramp setting (for references and summary, see Long and Copper, 1994) (Fig. 1). The Anticosti Island succession consists of subtidal (< 50 m deep) deposits, which can be subdivided into reef, sandy off-reef (interbedded calcarenites and micrites), and muddy off-reef (micrites and siliciclastic mudstones) facies. Reefs occur at five levels throughout the Ordovician-Silurian sequence. Tabulate and rugose corals, stromatoporoids, and calcareous algae are the dominant constructors of small bioherms and large patch reefs, but they are also abundant in the sandy and muddy off-reef facies. Extinction events near the end of the Rawtheyan Age (Late Ordovician) eliminated a number of reef-building corals and sponges (Copper, 1994).

METHODS AND MATERIAL

Endolithic traces were measured from coral and stromatoporoid external surfaces, polished slabs and thin sections. Aperture size and cavity depth were measured with digital calipers (accurate to 10 μm). Density of each macroboring and embedment structure was determined by counting surface apertures centered within a 4 square cm grid. Macroborings (diameter > 0.5 mm) were identified in 1,070 of 2,528 colonies of massive tabulate corals and stromatoporoids. Two embedment structures could not be referred to currently recognized ichnotaxa, and are designated Type 1 and Type 2 cavities. Samples used in this study are deposited in the research collection of the Department of Earth Sciences at Laurentian University, Sudbury, Canada.

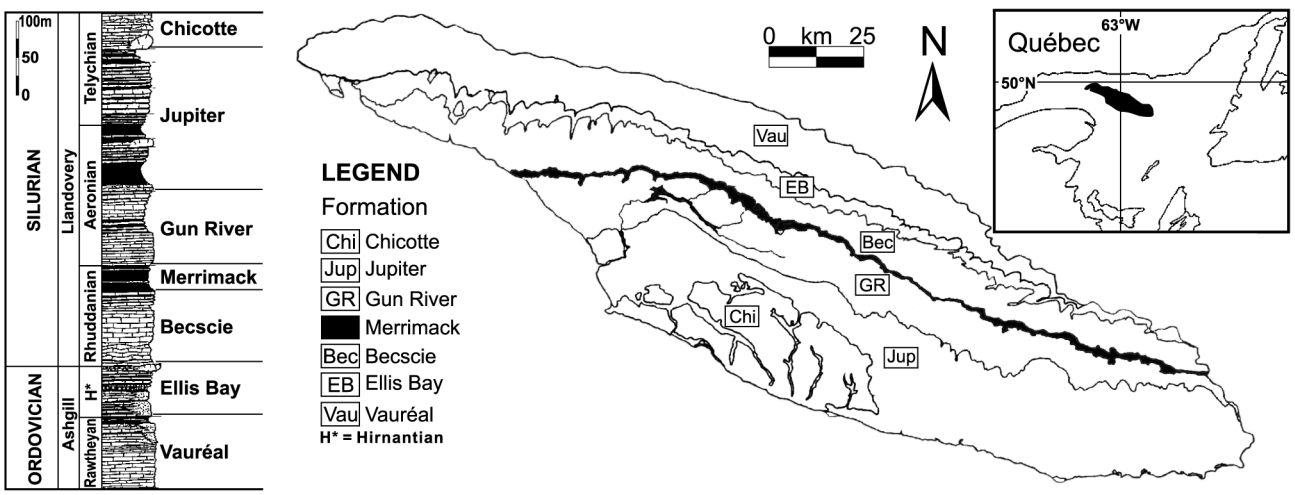

Figure 1. Stratigraphic column and geologic map of Anticosti Island, Québec, eastern Canada.

Table 1. Summary of four endolithic trace fossils from Anticosti Island.

	Trypanites	*Petroxestes pera*	*Type 1 cavity*	*Type 2 cavity*
Trace type	macroboring	macroboring	embedment	embedment
Aperture size ranges (mm)				
Width	0.65 - 9.53	3.01 - 6.62	0.28 - 2.96	1.24 - 3.43
Length	0.65 - 9.53	13.29 - 48.11	0.36 - 5.67	1.67 - 4.90
Maximum depth (mm)	52.81	14.53	35.98	26.67
Maximum density (per 4 cm²)	35	2	10	7
Width/Length ratio at aperture	~1	0.05 - 0.3	0.6	0.7
Occurrence in				
host substrate	not specific to any host	only in *Clathrodictyon*	only in *Columnopora*	only in ?*Propora* & *Clathrodictyon*
facies	reef & off-reef	only off-reef	only in reef	only off-reef
geologic stage	Rawtheyan to Telychian	Aeronian	Rawtheyan	Aeronian
Commonality (no. samples)	common (1065)	rare (5)	rare (4)	rare (9)

DESCRIPTION OF ENDOLITHIC TRACES

Four recurring types of endolithic trace fossils, including two macroborings and two embedment structures were identified in corals and stromatoporoids from Anticosti (Table 1).

Trypanites ispp.

With a wide size range, *Trypanites* have a circular aperture that most commonly is 2 to 3 mm in diameter (Fig. 2). The unlined cylindrical boring is straight to slightly curved with no appreciable swelling toward the rounded base. *Trypanites* was found in all types of corals and stromatoporoids examined in this study. *Trypanites* were concentrated on the upper surface of the host. Borings deep inside the host were mostly concentrated along horizons that apparently signify death and overgrowth surfaces. Surface boring density increased towards topographic highs, and most borings occurred within 1 cm of the bored surface. Undersurface borings were relatively uncommon, except in bulbous-shaped coral and stromatoporoid hosts. Maximum boring density was as high as 35 *Trypanites* per 4 square cm. Borings were found in equal abundance in Ordovician and Silurian samples. All of the studied facies contained corals and stromatoporoids that were infested with *Trypanites*. Most borings were formed in a dead host, but occasionally live hosts were bored, as evidenced by deflected host growth. *Trypanites* co-occurs with Type 2 cavities and *Petroxestes pera* but not with Type 1 cavities. Some *Trypanites* contain lingulids in life position, similar to those found in Type 2 cavities. These are interpreted as nestlers, not true borers, in the *Trypanites*. No attempt was made to differentiate ichnospecies of *Trypanites* for this study. *Trypanites* is distinguished from *Gastrochaenolites* by its lack of a basal swelling. No *Gastrochaenolites* were observed in this study.

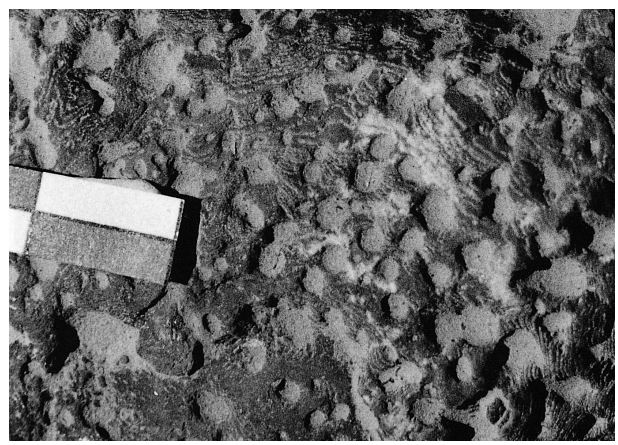

Figure 2. Densely bored (*Trypanites*) surface of host stromatoporoid, *Clathrodictyon*. Sample #1219, Locality A1211, Goéland Member, Jupiter Formation. NTS 12E/1 42400:51370. Scale bar has 1 cm divisions.

Figure 3. Large slot-shaped Petroxestes pera in *Clathrodictyon* (stromatoporoid). Sample #1014, Locality A1109c, Goéland Member, Jupiter Formation. NTS 12E/1 45280:55100. Scale bar has 1 cm divisions.

Petroxestes pera WILSON and PALMER

Petroxestes pera has an elongate, parallel-sided aperture typically longer than 20 mm and less than 6 mm wide. The unlined borings are slot-like with variable depth, terminating in a rounded base. *P. pera* was found only in *Clathrodictyon* stromatoporoids of the muddy Goéland Member of the Jupiter Formation (Fig. 3). All *P. pera* are found at the upper surface of the host skeleton and are often clustered subparallel to each other with a minimal spacing of 5 mm between aperture perimeters. All *P. pera* borings appear to have been made after the death of the host. The apparent confinement of *P. pera* to *Clathrodictyon* is likely due to the abundance of that stromatoporoid in the Goéland Member. Some *P. pera* co-occur with *Trypanites* and Type 2 cavities. In such instances, *P. pera* often truncated, and therefore post-dated, *Trypanites*. No shell material of a possible borer has been found in *P. pera*.

Described previously from the Late Ordovician (Pojeta and Palmer, 1976; Wilson and Palmer, 1988), this is the first report of *Petroxestes pera* from the Silurian (Aeronian Stage). *Corallidomus scobina*, a modiomorphid bivalve, was thought to be the creator of the Ordovician *P. pera* (Pojeta and Palmer, 1976), but no bivalve shell material was preserved in the Anticosti Island samples. No bivalve borings have been found in the time interval between the Ordovician *P. pera* and *Gastrochaenolites* reported from the Carboniferous (Wilson and Palmer, 1998).

Type 1 cavities

Type 1 cavities have an aperture with a biconvex outline that is generally not wider than half a centimeter (Fig. 4). The path of the cavity is straight to slightly sinuous and tapers greatly toward the narrow cylindrical base (Fig. 5A). Walls surrounding the cavity are of continuous trabecular calcite with a minimum thickness of 130 µm. Type 1 cavities were found only in one genus of tabulate coral, *Columnopora*. The cavities are exposed most frequently at the upper surface of the coral; never on the underside. Cavities run parallel to the growth axis of the corallites, deflecting two or more adjacent corallites. Up to 10 lenticular apertures occur per 4 square cm of the host *Columnopora* surface. All four *Columnopora* found with Type 1 cavities are from one reefal locality of Rawtheyan age (A14, =A1399 of the Mill Bay Member, Vauréal Formation). No other endolithic traces have been found co-occurring with Type 1 cavities in *Columnopora*. No evidence of the tracemaker has been found in these cavities.

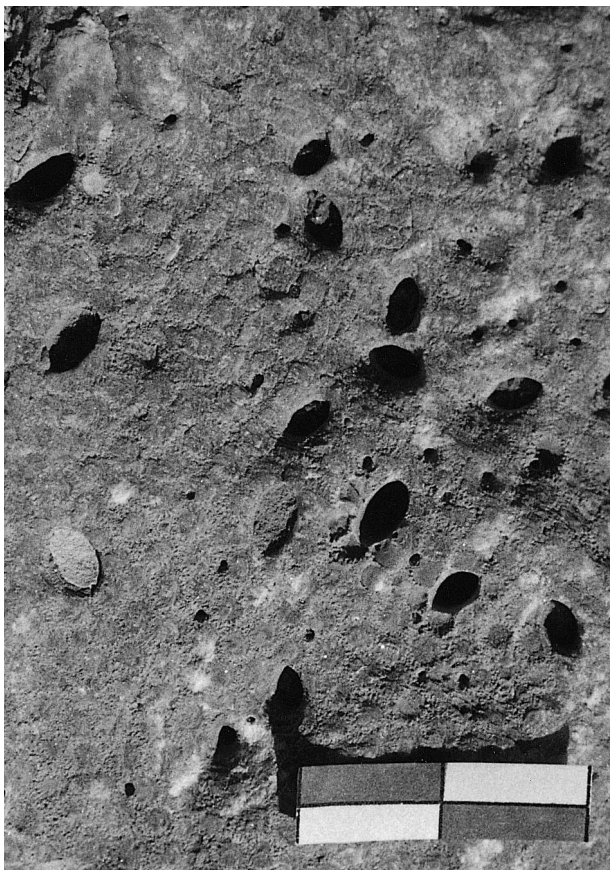

Figure 4. Biconvex outline of Type 1 cavity aperture at surface of *Columnopora* (tabulate coral). Sample #1048, Locality A1399, Mill Bay Member, Vauréal Formation. NTS 12E/14 73800:10750. Scale bar has 1 cm divisions.

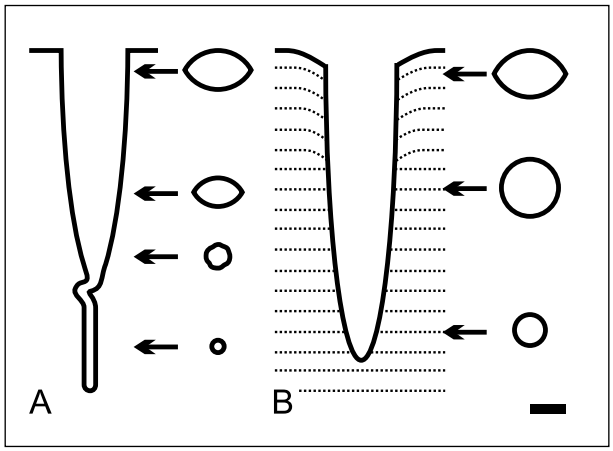

Figure 5. Schematic longitudinal sections of Anticosti embedment structures with select cross-sections (arrows). A, Type 1 cavity walled by host coral skeleton. B, Type 2 cavity in host stromatoporoid characterized by basal truncation of host laminae (dashed lines) and deflected laminae toward the aperture. A lingulid brachiopod (not shown) is commonly found in life position in Type 2 cavities. Scale bar = 1 mm.

The deflection of corallites and the trabecular microstructure of the cavity walls suggest that the Type 1 cavity may have been formed by the deflection of host coral skeleton around an endolithic organism. Similar endolithic cavities walled by host skeletal elements (e.g. *Chaetosalpinx*) have been reported from Silurian and Devonian favositid corals (Sokolov, 1948; Plusquellec, 1968; Stel, 1976; Oekentorp and Brühl, 1999). *Chaetosalpinx* are straight to sinuous cylindrical cavities with a narrow (0.1 to 1 mm) circular cross-section. These are proposed to have been formed by the host coral in response to an endosymbiotic organism. Type 1 cavities differ from *Chaetosalpinx* in having a larger diameter and distinctive lenticular aperture.

Type 2 cavities

Type 2 cavities have an aperture with a biconvex outline that is less than 5 mm wide (Fig. 6). The unlined Type 2 cavity is straight to slightly curved, tapering into a rounded base. In cross-section, the cylindrical cavity is lenticular nearest the aperture, but circular nearest the base (Fig. 5B). Host skeletons include *Clathrodictyon* and a heliolitid coral (*?Propora*). Nine samples (8 *Clathrodictyon*, 1 heliolitid) from muddy off-reef facies of the Goéland Member (Aeronian Stage) contained Type 2 cavities. All Type 2 cavities are found at the upper surface of the host skeleton and are oriented roughly parallel to the growth axis of the host. Up to 7 lenticular apertures occur per 4 square cm. Deflection of the host near the cavity is not constant with depth. Nearest the lenticular aperture, deflection occurs, but toward the base of the cavity, skeletal laminae are truncated and not deflected. The Type 2 cavity may be a *Trypanites* boring which has been extended vertically (upwards) by the deflection of the growing host skeleton. Nearly all Type 2 cavities contain a lingulid shell, preserved in life position. Apart from shallow pedicle scars of rhynchonellidae and terebratulidae (*Podichnus*; Bromley and Surlik, 1973), no mechanism for bioerosion is known in brachiopods. Therefore, the lingulids contained in Type 2 cavities are considered nestlers, and not excavators of the cavity base. However, it is considered possible that the lingulids may have been capable of deterring overgrowth of the Type 2 cavity by the living host skeleton. The distinct lenticular aperture of Type 2 cavities resemble the cross-sectional anterior outline of the lingulid valves. In some *Clathrodictyon* samples, only Type 2 cavities are present at the surface. More commonly, Type 2 cavities occur with *Trypanites* and occasionally with *Petroxestes pera*. Type 2 cavities are distinguished from Type 1 cavities by the truncation of the host skeleton near the base of the cavity.

Figure 6. Biconvex outline of Type 2 cavity aperture at surface of *Clathrodictyon* (stromatoporoid). Sample #1022, Locality A1179, Goéland Member, Jupiter Formation. NTS 12E/1 43220:52300. Scale bar has 1 cm divisions.

DISCUSSION

The ubiquity of *Trypanites* among bored tabulates and stromatoporoids, in reef and off-reef facies from all formations of the Late Ordovician-Early Silurian sequence of Anticosti Island, had a strong influence on bioerosion. *Trypanites* producers appeared to have been unaffected by the Late Ordovician mass extinction in their abundance. It is likely that the nonspecificity of *Trypanites* in substrate selection, including both skeletal and hardground surfaces, is the reason for their persistence through times of environmental stress. Neither the tabulate coral genus *Columnopora* nor Type 1 cavities are found in strata younger than the Ordovician. It is likely that the producers of these host-specific cavities were more susceptible to environmental catastrophes which targeted their preferred host substrates.

Nield (1984) has suggested that, in addition to selecting favourable water currents, larvae of the *Trypanites* producers concentrated on topographic highs. The latter has been observed in this study, where borings are concentrated in the uppermost centimeter of the upper death surface of the host substrate. In the absence of a living host, hard substrates may be more readily covered by sediments and encrusters, limiting access for bioeroders. With gradual sedimentation, topographic highs would be exposed longest, allowing more time for bioerosion.

A limited diversity of macroborings are recognized to include *Trypanites* and *Petroxestes pera*. No *Gastrochaenolites* or sponge borings were identified in this study. Evidence of hard substrate grazers, such as radulation traces of mollusks, was also absent in this study. *Trypanites* accounted for more than 99% of macrobioerosion in Anticosti corals and stromatoporoids, in striking contrast to modern settings, where excavations by sponges, bivalves, and epifaunal grazers are important (Hutchings, 1986; Edinger, 2000).

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